The Role of Behavior in Determining the Intertidal Zonation of *Littorina planaxis* Philippi, 1847, and *Littorina scutulata* Gould, 1849

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(8 Text figures)

INTRODUCTION

Littorina planaxis Philippi, 1847, and *L. scutulata* Gould, 1849, are common upper littoral gastropods of the west coast of North America. *Littorina planaxis* occurs higher intertidally than *L. scutulata,* being found on the highest rocks in the splash zone. The purpose of this study was to investigate those behavioral factors which might limit the vertical distribution of both species in the vicinity of Bodega Head, California.

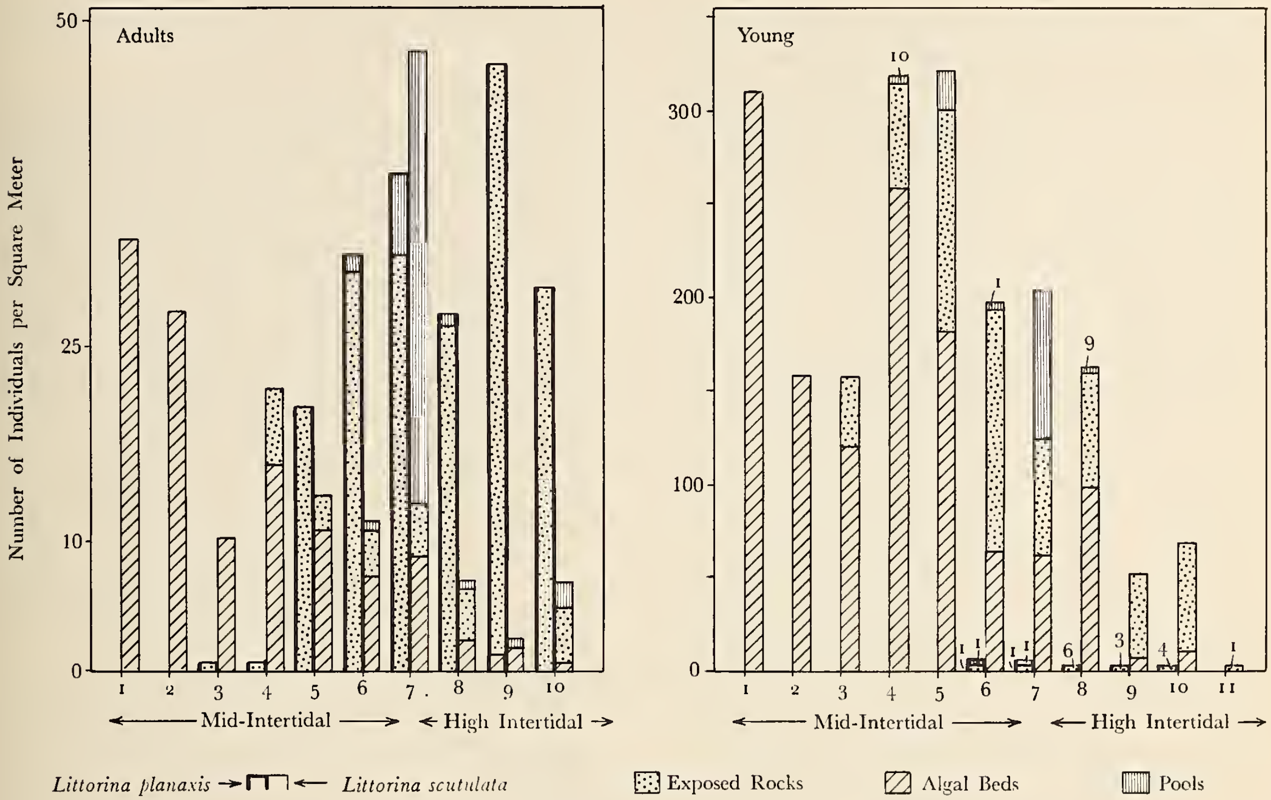
HABITAT PREFERENCE

Hewatt, 1937, and Ricketts & Calvin, 1952, describe *Littorina planaxis* as a dominant species on the rocky intertidal Zone I (above mean higher high tide) and *L. scutulata* as characteristic of Zone II (between mean higher high and mean lower high tides). There is considerable variation in the tidal range of both species, but this undoubtedly relates to the degree of exposure and concomitant wave splash in the individual study areas. *Littorina planaxis* occurs almost exclusively on those exposed rocks which are wetted only by splash, and which are free of macroscopic algae (Hewatt, *op. cit.*; Dahl, 1964). The habitat of *L. scutulata* appears more variable. Dahl and Hewatt report it in beds of algae and also occasionally in beds of *Balanus glandula* Darwin, 1854.

In order to determine the distribution of the two littorines at Bodega Head, we conducted counts along two transects running from the high intertidal down through the mid-intertidal region. This spanned the ranges of both species. The results for adults and for young are plotted in Figure 1. The number of individuals was counted in each square meter along the transects, and these counts were combined into twelve equal groupings such that the two transects, although of different lengths, could be represented in a single graph.

Adult *Littorina planaxis* clearly occupy a higher position than *L. scutulata* (Figure 1). We found *L. planaxis* almost exclusively on exposed rocks wetted at high tide by splash and the larger waves. *Littorina scutulata* were most abundant in beds of macroscopic algae, especially *Pelvetiopsis limitata* (Setchell) Gardner, 1910, but they were also common in high tide-pools. These pools were usually rimmed with *Gigartina papillata* (C. A. Agardh) J. G. Agardh, 1846, and it was here that *L. scutulata* congregated. The lower limits of *L. scutulata* came abruptly in each transect as the relatively exposed beds of algae gave way to deep pools or channels.

Curiously, almost no small *Littorina planaxis* were found, and yet the small *L. scutulata* greatly outnumbered the adults (Figure 1). Also, we found many young *L. scutulata* occurring higher up than the adults of the same species (*cf.* data in Figure 1). They were found commonly on exposed rocks along with adult *L. planaxis.* They were usually in small crevices in the rocks or packed into old *Balanus glandula* tests, as reported by Hewatt, *op. cit.*, for the Monterey coast. However, in contrast to the findings for the Monterey region, adult *L. scutulata* were not common in barnacle beds at Bodega.



	Littorina planaxis		*Littorina scutulata*	
	Adults	Young	Adults	Young
rocks	394	21	51	1345
pools	16	1	83	259
algae	3	1	250	3011
	n = 413	n = 23	n = 384	n = 4615

Figure 1

Distribution of *Littorina* in the rocky intertidal area

Three types of factors could be involved in the zonation and habitat preferences of *Littorina planaxis* and *L. scutulata*. First, the physiological tolerances of the species to one or more physical parameters of the environment might act as limiting factors to distribution. Second, biotic characteristics such as predation, competition, and available food could cause one region to be preferable to another. The next section summarizes the available data on physical and biotic factors which may influence the distribution of the two littorines. While these biotic and abiotic factors must be the ultimate causes of the distribution patterns, it is possible that the behavior of the littorines prevents their movement into those areas where conditions would be unfavorable. Our research centered on the third possibility and the results are presented in "Behavioral Limits to Distribution."

POSSIBLE ENVIRONMENTAL FACTORS LIMITING DISTRIBUTION

Desiccation: Since *Littorina scutulata* does not occur as high intertidally as *L. planaxis*, the possibility exists that the upper limits of the former might be a function of greater vulnerability to temperature or desiccation, or both. Bowlus, 1966, studied water loss in *L. planaxis* and

L. scutulata; all animals were held in dry containers at temperatures varying from 29.4° C to 32.2° C. At 100 hours *L. scutulata* had begun to die and by 127 hours 70% were dead. In the same time period, none of the *L. planaxis* had died, and they lost much less body water. *Littorina planaxis* secretes a mucous seal between the shell and substrate when exposed to dry conditions. We did not observe this response in *L. scutulata,* but it undoubtedly would help prevent water loss. Hewatt, *op. cit.*, recorded 100% survival of *L. planaxis* above the highest wave splash for at least 64 days. Barkman, 1955, gathered similar data for many littorines and was able to correlate, in a general way, desiccation tolerance with the degree of periodic exposure experienced by each species.

Although it appears that *Littorina planaxis* is more resistant to high temperatures and dry conditions than is *L. scutulata,* we shall show that the behavior of the latter protects it from these circumstances.

Submersion: Ricketts & Calvin, *op. cit.*, state that *Littorina planaxis* will "ultimately drown" if held under water. Many species of high intertidal periwinkles, including *L. planaxis,* have relatively degenerate ctenidia and a vascularized mantle epithelium, both of which favor oxygen exchange in air (Nicol, 1960). Thus drowning or at least respiratory inefficiency under water may be a factor controlling the lower limits of distribution in *L. planaxis*.

Fresh Water: Since *Littorina planaxis* occurs higher than *L. scutulata,* and since considerable rainwater can accumulate in the high intertidal, it might be expected that the former species would be more tolerant to fresh water. In the laboratory, we found only one percent mortality in *L. planaxis* after 3 days submersion in tap water (n = 100), while 65% of the *L. scutulata* died in 2 days. Seventy-five percent of these had burst from their shells, presumably due to osmotic stress. Water circulation was maintained during the experiment. Barkman, *op. cit.*, in a survey of other littorine studies, found that species which occupy the upper zones tend to have greater fresh water tolerances.

Hypersalinity: In the summer, the highest tide-pools at Bodega Head become hypersaline between spring tides due to evaporation. Although we have no experimental data regarding tolerances, littorines are absent from many of these pools. We have found *Littorina scutulata* common in pools with salinities up to 104% sea water, only rarely in those of 110%, and not at all in pools of about 140%.

Competition and Predation: The behavioral experiments described in the following section suggest that competition is not the immediate cause of behavioral zonation, since both *Littorina planaxis* and *L. scutulata* selected their respective habitats in the absence of one another. Nevertheless, this does not rule out the possibility that competition in the past has resulted in selection for such behavioral responses.

Littorina planaxis occurs above the predatory snail *Thais emarginata* (Deshayes, 1839) in the intertidal, but there is no evidence to suggest that this results from predatory exclusion.

Food: Dahl, *op. cit.*, noticed that *Littorina planaxis* occurred largely on high exposed rocks with encrustations of microscopic algae, while *L. scutulata* were common at lower levels in beds of macroscopic forms; however, it remains unclear whether this apparent difference in food preference is a cause or result of differences in zonation. Dahl did find that *L. planaxis* were unwilling or unable to feed on the large algae unless the fronds were chopped into small pieces; this suggests that food might be a zonation factor, at least for this species.

Table 1 summarizes those environmental factors which may be involved in controlling the limits of distribution in the two littorines.

Table 1

Possible Environmental Factors Controlling the Distribution of *Littorina*

	Upper Limits	Lower Limits
Littorina planaxis	1. permanent desiccation above splash zone	1. possible respiratory inefficiency during submersion
	2. lack of algae as food above splash zone	2. possible lack of microscopic algae as food 3. possible predation 4. possible competition
Littorina scutulata	1. desiccation on exposed rocks 2. fresh (rain) water on exposed rocks	1. possible lack of suitable foods 2. possible respiratory inefficiency during submersion
	3. hypersaline waters of highest pools 4. lack of macroscopic algae for food	

BEHAVIORAL LIMITS TO DISTRIBUTION

Field Studies

In attempting to evaluate the role of behavior in the distribution of *Littorina planaxis* and *L. scutulata,* we carried out a field experiment at Doran Beach involving transplantation of marked animals. Region 1 (Figure 2) encompassed a small tide-pool rimmed with *Gigartina,* and ran up about 2 m onto an exposed rocky shelf. *Littorina scutulata* were common in and around the pool while *L. planaxis* occurred on the rock face above. We placed 75 *L. planaxis* and 50 *L. scutulata* (marked with red or yellow enamel) in the pool and equal numbers up on the rocks. This is the situation represented at day one in Figure 2. Region 2 (Figure 3) was similar except that the exposed rock face gave way to an extensive bed of *Pelvetiopsis* instead of a tide-pool. Also, region 2 experienced a much greater wave splash during high tides.

Since our habitat work showed that *Littorina planaxis* was common on exposed rocks while *L. scutulata* occurred in pools and beds of algae, we felt that the outcome of this experiment would indicate the possible role of movement in zonation. If the littorines segregate according to habitat, those *L. planaxis* placed high should remain there, while those placed in pools (region 1) or algae (region 2) should

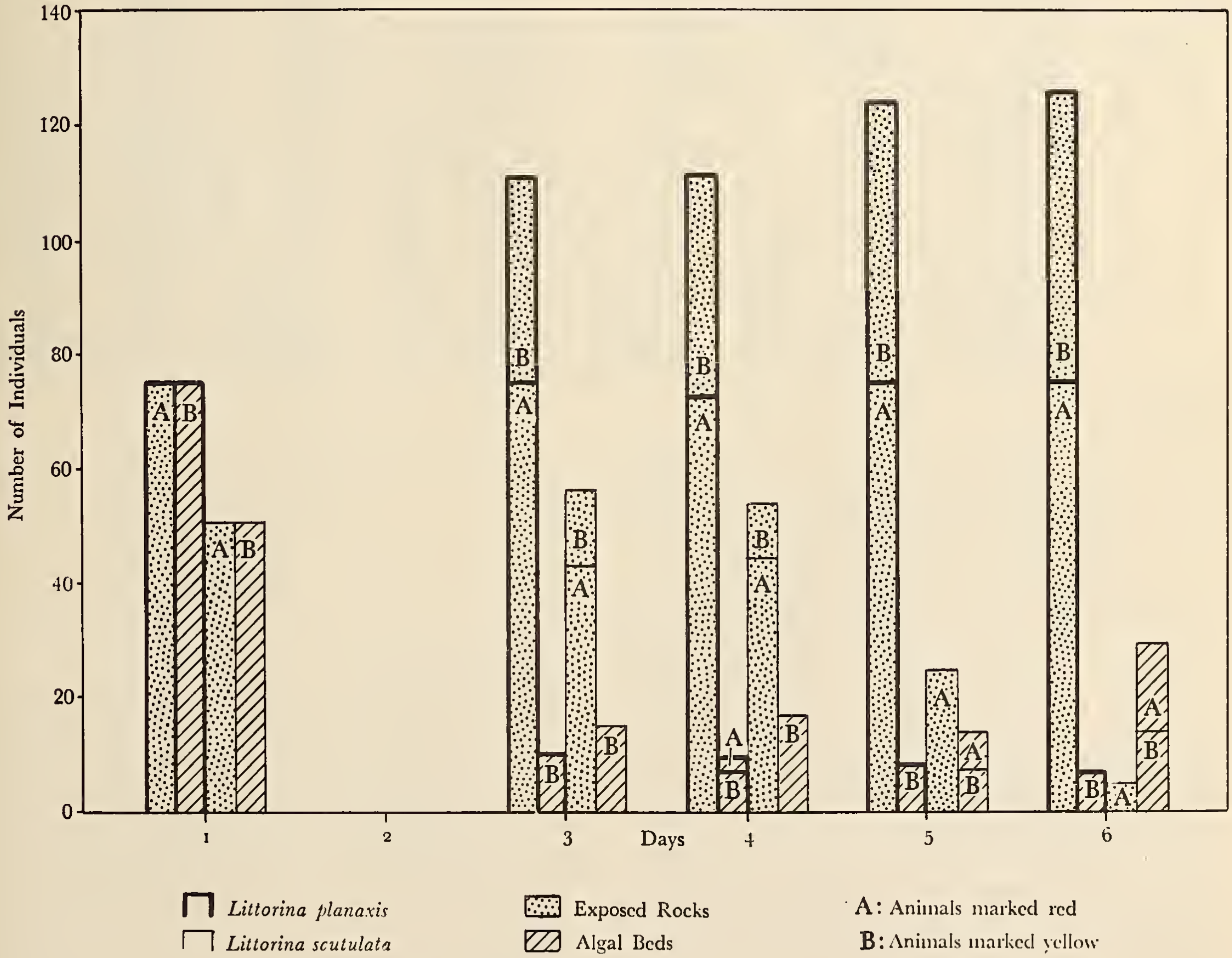


Figure 2

Doran Beach. Habitat selection study, region 1

Figure 3

Doran Beach. Habitat selection study, region 2

move up to the exposed rocks. The reverse would be expected for *L. scutulata*. Results (Figures 2 and 3) show that this is essentially what happened, and we conclude that behavioral zonation occurs.

Littorina planaxis moved up rapidly in both areas, although a small percentage was apparently swept away before becoming established. The behavioral response of *L. scutulata* was not as immediate. Also, a larger percentage was washed away; both those placed on exposed rocks and those in pools or algae were lost. It is highly significant that the downward trend of *L. scutulata* was slower in region 1 than in region 2 (*cf.* Figures 2 and 3). We attribute this to the combined effects of voluntary downward movement and involuntary movement due to heavier wave shock in the latter region. *Littorina scutulata* were easily dislodged from the high rock by wave action; they then tumbled down into the *Pelvetiopsis*. The response in region 1 represents largely behavioral movement alone, as this region was protected from strong wave action.

We next conducted a series of experiments at Bodega Head, designed to analyze in more detail the responses of *Littorina* when placed in a variety of habitats. These experiments are represented in Figures 4 through 7, and involve distances traveled by each species in relation to the tide cycle. Each species was tested separately in order to prevent possible interactions. Snails were marked with enamel and counted periodically during the trial without being removed from the substrate.

1. Thirty *Littorina planaxis* and 42 *L. scutulata* were placed about 35 cm above the surface of a high tide-pool on an exposed rock (Figure 4). Although *L. planaxis*

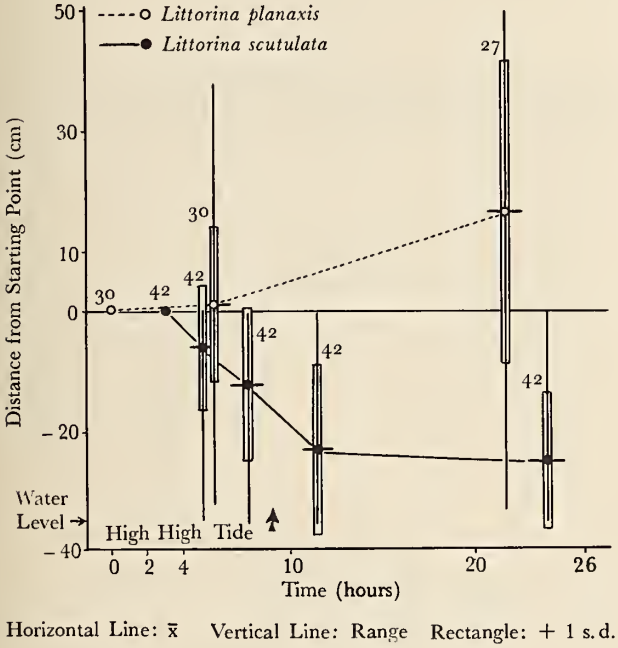


Figure 4

Movement of *Littorina* placed above a high tide-pool

moved in all directions (range: −33 cm to +56 cm), they averaged 16.8 cm higher on the rock after 22 hours. In *L. scutulata* there was an obvious downward movement, averaging 25.3 cm below the starting point after 24 hours. This position was only about 7.6 cm above water level; the majority of the snails came to rest on the *Gigartina* around the lip of the pool. This difference is highly significant at the 0.01 probability level, using a two-sided "t"-test for differences of means, and indicates a movement of *L. scutulata* down towards the pools in the high intertidal.

2. Figure 5 shows the results of a related experiment in which 70 *Littorina planaxis* and 42 *L. scutulata* were set in the bottom of a tide-pool. All animals in the pool were given the value zero cm. After 48 hours, *L. scutulata*

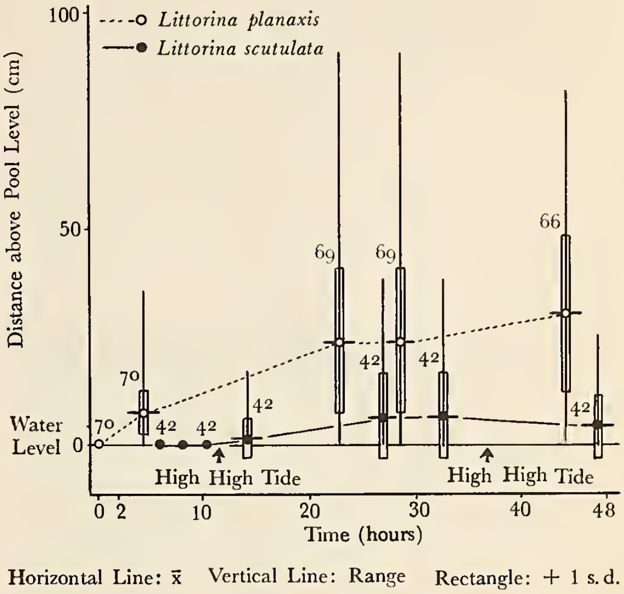


Figure 5

Movement of *Littorina* placed in a high tide-pool

averaged 7.26 cm above pool surface, very comparable to the position of this species in the first experiment; during the same period, *L. planaxis* moved up an average of 32 cm. Again, *L. scutulata* selected the pool rim, while *L. planaxis* moved out on the exposed rocks. It is significant that movements ceased when the rocks were dry between higher high tides (Figure 5).

3. In the two preceding experiments, we demonstrated behavioral differences between the two littorines in the high intertidal. The final two experiments were conducted at the lower limits of distribution. First, we placed 45 *Littorina planaxis* and 55 *L. scutulata* on a rock slope with scattered algae. This was within the normal range of *L. scutulata*. The results (Figure 6) show a significant (to 0.01 level) upward movement of *L. planaxis* when compared to the other periwinkle. We interpret this as evidence of *L. planaxis* seeking its preferred, higher, intertidal position. Note here that the movement occurred between high tides rather than during them. The snails clung firmly in place during the periods of wave shock.

4. The final experiment was carried out at a level comparable to that of the last, but on an exposed point subject to very heavy splash and surge; macroscopic algae were lacking. Here both species moved up to a higher

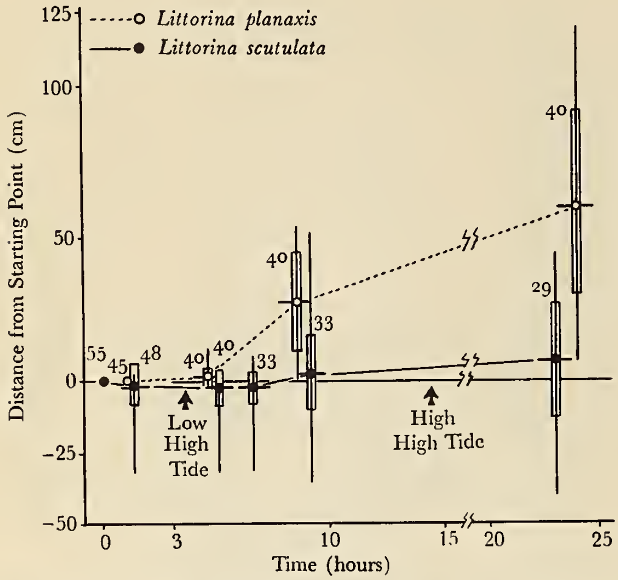


Figure 6

Movement of *Littorina* placed in a bed of macroscopic algae

position (Figure 7); there was no significant difference in means at the 0.05 level. This area, then, was apparently below the preferred habitat of either species.

We noticed in the Doran Beach study that *Littorina scutulata* were more easily dislodged than *L. planaxis.* Data from the last series of experiments support this and suggest two ways in which the latter is better adapted. First, when *L. scutulata* become dry on an exposed rock, instead of fastening on with a mucous seal as *L. planaxis,* they come to lie with opercula facing up and the shell attached by only a thin strand of mucus. In this position, *L. scutulata* are easily dislodged. Splash thus accounted for a considerable proportion of the downward movement of *L. scutulata* in the first experiment (Figure 4).

Second, in the two experiments concerning exposed lower areas, 13% of 69 *Littorina planaxis* were swept away while 41% of 79 *L. scutulata* were lost. Since these areas were continuously moist, the snails did not withdraw into their shells, but simply clung to the rocks. It would appear that *L. planaxis* is better able to do so, although North, 1954, found relative foot size to be comparable in both species. North found that greater numbers of *L. planaxis* were lost from a rock which he washed through a tide-pool. Our data, collected under more natural conditions, suggest a greater resistance to wave shock in *L. planaxis* – certainly an essential adaptation for life on exposed rocks.

In summary, *Littorina planaxis* and *L. scutulata* apparently occur in their respective habitats largely because of differences in behavior.

We found *Littorina planaxis* will move up out of pools or beds of macroscopic algae; thus these constitute the lower limits of their distribution. Williams, 1950, found he could induce *L. planaxis* to move higher than they normally occur in the field by artificially wetting the substrate. This suggests that these snails will move as high as there is wave splash. Williams reports that *L. planaxis*

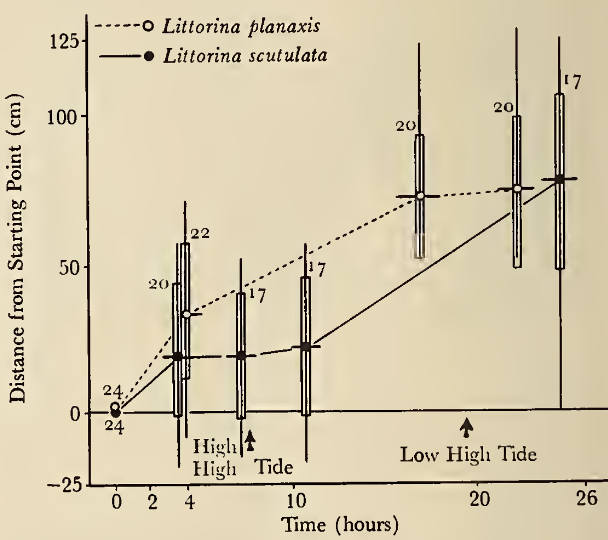


Figure 7

Movement of *Littorina* placed on a low intertidal rock

will move back down from a high position if they have experienced a period of desiccation. Thus it may be that populations fluctuate with the high tide levels. *Littorina scutulata* avoids both high rocks and lower areas by selecting pools and beds of algae in the mid-intertidal.

Evans, 1961, attributed behavioral zonation in *Littorina punctata* Ferrusac, 1821, to a combination of geotaxis and orientation to the shore. BARKMAN, *op. cit.*, and NEWELL, 1958 a, 1958 b, considered gravity, light, tidal fluctuations, and preference for certain algae to be involved in the zonation of *L. obtusata* FERRUSAC, 1821, and *L. littorea* FERRUSAC, 1821. In the following section we have attempted to evaluate the role of various environmental stimuli which might affect the behavior of *L. planaxis* and *L. scutulata*.

Laboratory Studies

The Role of Algae: In the field adult *Littorina scutulata* are most abundant on *Pelvetiopsis limitata*, somewhat less common on *Gigartina papillata*, and occur only rarely on other species of algae. At least two explanations for this distribution are possible. *Littorina scutulata* may choose certain species of algae in preference to others or they may choose a certain intertidal level regardless of the type of algae present. Three sets of experiments were set up to test the first alternative.

1. An aquarium ($33 \times 53 \times 127$ cm) was set up following the procedure of BARKMAN, *op. cit.*, and VAN DONGEN, 1956. There was only a shallow layer of water on the bottom which ran from an inlet at one end to an outlet at the other. One species of alga was placed at the inlet with a concrete block placed on each side to prevent the algae from washing down the aquarium (*cf.* diagram in VAN DONGEN). One hundred *Littorina scutulata* were placed 41.5 cm downstream from the algae. Controls were run in which no algae were present. All trials lasted for 12 hours and each of the 4 species of algae was run twice. The bottom of the tank was scrubbed after each run to prevent the periwinkles from detecting the scent of algae or their own mucus trails. Results were recorded in 4 categories: those snails which were on the algae, those that moved upstream but were not found on the algae, those which remained in the starting area, and those which moved away.

Results of this experiment (Table 2) show that *Littorina scutulata* moves toward *Gigartina* and *Pelvetiopsis* in greater numbers than toward *Iridophycus flaccidum* SETCHELL & GARDNER, 1937, and toward the latter in greater numbers than toward *Prionitis lanceolata* HARVEY, 1853. These differences are all significant at greater than the 0.001 level by the chi-square test. There was no significant difference between *Pelvetiopsis* and *Gigartina*. The number moving upstream but not found on the algae remained

Table 2

Attraction of *Littorina scutulata* to Single Species of Algae when Placed Down-Stream from the Algae

	Up-Current		Central	Down-Current	Total
	on algae	not on algae			
Control:					
trial 1	0	35	41	24	100
trial 2	0	41	27	32	100
Total	0	76 (38%)	68 (34%)	56 (28%)	200
Pelvetiopsis limitata					
trial 1	44	32	8	15	99
trial 2	30	50	1	19	100
Total	74 (37%)	82 (41%)	9 (5%)	34 (17%)	199
Gigartina papillata					
trial 1	34	34	9	16	93
trial 2	32	46	9	13	100
Total	66 (34%)	80 (41%)	18 (9%)	29 (15%)	193
Iridophycus flaccidum					
trial 1	14	45	31	7	97
trial 2	23	34	13	22	92
Total	37 (20%)	79 (42%)	44 (23%)	29 (15%)	189
Prionitis lanceolata					
trial 1	5	31	9	52	97
trial 2	8	77	2	15	102
Total	13 (6%)	108 (54%)	11 (5%)	67 (34%)	199

nearly constant throughout the runs except in the *Prionitis* tests. For unknown reasons the second of the two *Prionitis* runs differed significantly from the first and caused this upstream non-algae value to be high.

When no algae were present, 38% of the *Littorina scutulata* moved upstream; when algae were present, 60% or more moved upstream except in the one run using *Prionitis*.

2. The second set of experiments, similar to another series carried out by BARKMAN, *op. cit.*, and VAN DONGEN, *op. cit.*, was conducted on the bottom of two large tanks, each of which had a shallow layer of water running over the bottom. One hundred *Littorina scutulata* were placed on the bottom in the center and four patches of algae were each placed at 15 cm distance form the *L. scutulata*. At the end of 12 hours the number of animals on each species of alga was recorded, the bottom of the tank scrubbed, and the four algal species were rotated 90° so that after four trials each species had been in each position, thus eliminating any effects caused by unequal lighting, etc., on the tank floor.

Gigartina and *Pelvetiopsis* attracted the greatest number of periwinkles (Table 3), *Iridophycus* was second, and *Prionitis* was last. The difference between the first three and *Prionitis* was significant at the 0.001 level, but there was no significant difference between the first three. Nonetheless the order of preference was similar to that of the first experiment.

Table 3

Selection of Algae by *Littorina scutulata*
When Four Species of Algae are Presented Simultaneously

	Iridophycus	*Pelvetiopsis*	*Gigartina*	*Prionitis*	Wall	Total
Tank 1	21	38	16	3	20	98
	12	32	44	4	6	98
	9	15	36	24	11	95
	32	7	28	7	15	89
subtotal	74	92	124	38	52	380
Tank 2	35	30	15	1	15	96
	29	13	8	22	28	100
	11	33	30	13	13	100
	16	21	17	17	28	99
subtotal	91	97	70	53	84	395
Total	165	189	194	91	136	775
Percent of algae:	25.8	29.6	30.4	14.2		

3. In the third set of experiments two sheets of clean glass (22×52 cm) were placed in a small aquarium (30×38×61 cm) such that they formed a V at the bottom; the slope of each was 37° from the horizontal. An 8 to 10 cm band of a single species of alga was held on the upper surface of each plate 3 cm below the surface by a thread around each plate. In the absence of the algae, periwinkles placed under water in the V would climb out of the water to the top of one of the glass plates. However, with the algae present as described they would congregate on the algae, at least temporarily, rather than continue up the plate. Between 60 and 70 individuals were tested separately for each of four species of algae. After one hour the number of animals on the algae and above it was recorded, the glass plates were scrubbed, and fresh animals were started at the bottom.

Pelvetiopsis retained the greatest number of *Littorina scutulata* beneath the water (71%), *Gigartina* and *Iridophycus* were second (36 and 42%), and *Prionitis* was third (18%). The results are similar to the preceding experiments except that *Gigartina* dropped to second place with *Iridophycus*. The difference between *Pelvetiopsis* and the second two is significant to the 0.001 level, and between these two and *Prionitis* to the 0.01 level by the chi-square test.

The results of these three experiments show that the four algae are probably preferred by *Littorina scutulata* in the order: *Pelvetiopsis, Gigartina, Iridophycus, Prionitis.* On Bodega Head, *L. scutulata* was found on nearly every patch of *Pelvetiopsis* that we observed. *Gigartina* appeared to be occupied only when it was found at levels comparable to *Pelvetiopsis,* or when it was lining tide-pools. It was commonly found at lower levels and in more exposed sites without any periwinkles on it. *Iridophycus* was lower than *Pelvetiopsis* in the field, and *L. scutulata* was present on it only in those unusual locations where it occurred high. *Prionitis* was found in tide-pools and it only rarely had adult periwinkles on it.

When *Littorina scutulata* were placed in an aquarium the majority would quickly climb out of the water. Our laboratory experiments above have shown that the presence of *Pelvetiopsis* in the water will keep these animals below the water line. *Gigartina,* while preferred over the remaining two species of algae when at the surface, was not effective in keeping the periwinkles beneath the water; this might explain why *Gigartina* lacks periwinkles when it occurs low intertidally.

In order to test the effects of the interaction between water level and algae on the position of *Littorina scutulata,* the third experiment was modified. In this case the algae formed a 20 cm band extending equally above and below the water line. Color-marked individuals were placed in the bottom of the V, and their locations with respect to the water line were recorded every 1 or 2 hours, except during 8 hours of darkness each night. These figures were converted to an estimated time spent above or below water line on the algae (a separate set of experiments, testing the effect of tidal action independent of the position of macroscopic algae, will be described later).

It was found that all individuals (15) remained on the algae for the 75 hour duration of the study; most moved up and down, entering and leaving the water several times, but 3 apparently remained well above the water line throughout the test. *Littorina scutulata* were above the water 59% of the time, below 21% and at the water line 20%. This indicates that *L. scutulata* retains the tendency to move up out of the water when on *Pelvetiopsis* but that they will remain in the water rather than leave the algae.

These experiments indicate that *Littorina scutulata* select both the level and the species of algae on which they occur. Barkman, *op. cit.*, found a similar situation for *L. obtusata.*

On Bodega Head small (2-6 mm) *Littorina scutulata* occur in large numbers in tide-pools on *Prionitis lanceolata,* but adults are rarely found in this situation. Consequently we repeated the "V-glass" experiment with 77 young *L. scutulata* using *Prionitis* on the glass below water level. The results of this study showed that 79% of the young remained submerged for at least 1 hour on *Prionitis,* while only 18% of the adults did so.

Since *Littorina planaxis* is normally found above the level of macroscopic algae, the third experiment (V-glass) tried on *L. scutulata* was rerun on *L. planaxis.* Whereas *Pelvetiopsis* was sufficient to keep 71% of the *L. scutulata* beneath the water for an hour, it retained only 17% of 69 *L. planaxis* tested.

Dahl, *op. cit.*, has shown that *Littorina planaxis* will feed on chopped-up macroscopic algae, but rarely on whole fronds. He suggested 3 reasons for this behavior: (1) *L. planaxis* prefers a more stable substrate, (2) they are unable to bite off pieces of whole algae, (3) "most macroscopic algae are somehow chemically disagreeable." He eliminated the third possibility, since the snails did consume the chopped-up macroscopic algae. Dahl found that there were no obvious differences in the radulae of the two littorines, which makes the second reason unlikely. Therefore the type of substrate may be the stimulus to which *L. planaxis* responds. Apparently *L. planaxis* will continue to crawl upwards until it locates a suitable, (*i. e.* stable) substrate on which to feed.

In summary, *Littorina scutulata* display a strong negative geotaxis while in water; this is suppressed in the presence of certain preferred species of macroscopic algae. *Pelvetiopsis* is preferred by adults and *Prionitis* by young. The snails can distinguish the various species of algae and show a definite order of preference. Negative geotaxis continues in effect while *L. scutulata* is submerged; this tends to move the periwinkles to the highest macroscopic algae, which are usually also the preferred species. In contrast, *L. planaxis* displays a strong negative geotaxis which is not suppressed in the presence of macroscopic algae. Its usual food is microscopic encrusting forms occurring high intertidally.

Tidal Action: It has been shown in the laboratory that the presence of certain species of macroscopic algae will cause a separation in vertical location of *Littorina planaxis* and *L. scutulata*; however, other factors, such as tide, may also play a role in determining the separation seen in the field. In order to determine in the laboratory whether fluctuating water level alone would cause a separation of the two species, a large aquarium (113 × 113 × 179 cm) was set up in which water level was periodically raised and lowered. The "high tide" was 72 cm above the bottom and the "low tide" was 30 cm up, making a total range of 42 cm.

Both species were found over a wide range of heights (Figure 8), but it will be seen that there was an immediate separation of over two standard deviations between the average positions of the two species. *Littorina scutulata* occurred mainly around the mean "high tide" line. *Littorina planaxis* climbed higher out of the water and the majority was found at the top of the tank, where an overhanging lip kept them from moving higher. Neither species made vertical migrations with the artificial tides. *Littorina scutulata* became active each time the water reached their level, but most of the *L. planaxis* were a considerable distance above the water and remained dry and inactive.

Geotaxis: It has already been mentioned that both *Littorina planaxis* and *L. scutulata* climb up out of water when placed in an aquarium. Also we noted that certain species of macroscopic algae will override the negative geotaxis in *L. scutulata,* but that this geotaxis is still present, acting to move the animals up to the highest algae.

Since *Littorina planaxis* will continue to crawl upwards after leaving the water, it seemed likely that some environmental cue must prevent them from continuing to crawl up away from the ocean. In the field we noted that they would not continue to move up on dry rock and seemed to limit their activities to periods when the rocks were wet from the spray of high tide.

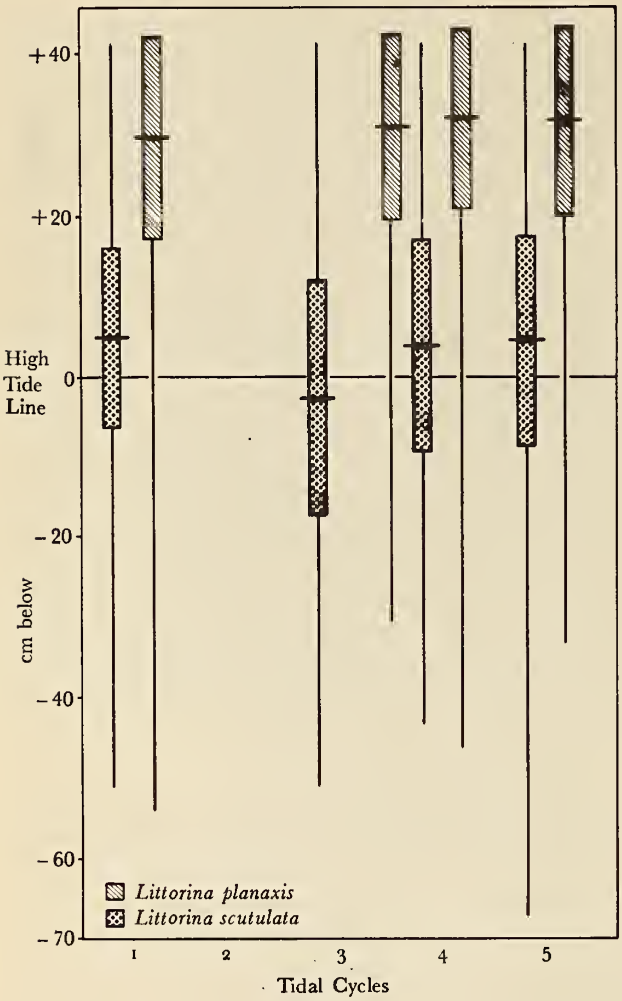


Figure 8

Movement of *Littorina* placed on bottom of tank with fluctuating water level

In the laboratory we found that *Littorina planaxis* would climb out of water and up a warm, dry glass surface as far as they were able to carry enough water with them to keep the glass moist. Those animals placed directly on a warm, dry surface closed up and did not move down. However, those animals that moved up from water onto a dry surface would turn and move down the glass if a blast of hot dry air from a hair dryer were directed toward them. A blast of cool air did not have this effect. Heating the glass ahead of the animal from the underside would also cause the snail to reverse directions and go down. Thus, a reversal of negative geotaxis in *L. planaxis* can be elicited when an animal climbing above water encounters unfavorable temperatures. Also, an animal desiccated for a considerable time will move down when rewetted. Studies by other workers have shown that many species of *Littorina* exhibit reversals of geotaxis after desiccation (Barkman, *op. cit.*; Newell, *op. cit.*; Janssen, 1960; Evans, *op. cit.*).

Light: Since *Littorina planaxis* and *L. scutulata* occur at different tidal levels, it seemed possible that their response to light might be one of the controlling factors. Eighty-seven *L. planaxis* and 85 *L. scutulata* were tested 3 times each for light response, using the same small aquarium and sloping glass plates which were employed in the third of the experiments with algae. A 100 watt bulb was placed at one end of the aquarium so that an animal climbing the glass plates would either be going directly toward the light or away from it. The light intensity varied from 400 foot-candles at the top of the nearest glass plate to 12 foot-candles toward the far end of the aquarium. *Littorina planaxis* proved to be strongly photonegative but *L. scutulata* was only slightly so (Table 4). We obtained similar results using 86 young *L. scutulata*. Smaller samples of each species were tested on a horizontal glass plate in the aquarium; results were similar.

Table 4

Responses to Light
by *Littorina planaxis* and *Littorina scutulata*

	Littorina[1] *planaxis* (adult)	*Littorina scutulata*[1] (young) (3½-6 mm)	(adult) (10- mm)
+ + +	2	10	13
+ + —	1	24	14
+ — —	13	29	32
— — —	71	23	26

[1] Numbers of individuals falling into each of the possible categories of response. + = movement towards, — = movement away from light. Each symbol equals one experiment and each animal was tested three times.

The experiments on sloping glass were rerun using strong natural light (15000 foot-candles) shining in at a similar angle and the results were practically identical to those with the weaker light. All experiments were run at water temperatures between 14 and 15° C.

The strong photonegative response of *Littorina planaxis* does not prevent it from moving up in the intertidal zone.

However, this species is found clustered in cracks and crevices, and light may be the stimulus causing this. Such behavior would likely be of survival value by reducing desiccation, heating, and predation. *Littorina scutulata* may show a weaker photonegative response because, in its more protected and wet location, a strong response would be of little value. However, the response may be sufficient to drive some animals under the protection of algal fronds.

Apparently most species of *Littorina* have distinct light responses, but these are not always correlated in any obvious way with behavior in the field (BARKMAN, *op. cit.*; NEWELL, *op. cit.*; JANSSEN, *op. cit.*; CHARLES, 1961 a, 1961 b, 1961 c).

Behavioral responses controlling distribution of *Littorina planaxis* and *L. scutulata* are summarized in Table 5.

Table 5

Behavioral Responses Controlling Distribution of *Littorina planaxis* and *Littorina scutulata*

	Upper Limits	Lower Limits
Littorina planaxis		
	Reversal of Geotaxis	Negative Geotaxis
	1. on reaching high temperatures	1. when under water
	2. when rewetted after desiccation	2. when on macroscopic algae
Littorina scutulata		
	Negative Geotaxis suppressed by preferred species of algae	Negative Geotaxis

SUMMARY AND CONCLUSIONS

1. *Littorina planaxis* and *L. scutulata* are common periwinkles of the rocky coast of California. *Littorina planaxis* occurs very high intertidally, usually on exposed rocks in the splash zone. *Littorina scutulata* is found largely in mid-intertidal areas, frequently in beds of macroscopic algae and pools rimmed with algae.

2. The physiology and food habits of each species are correlated with these differences in habitat. *Littorina planaxis* is more tolerant of desiccation, temperature, and fresh water, – conditions encountered more often in the high intertidal. *Littorina scutulata* readily consumes macroscopic algae, while *L. planaxis* apparently will take only microscopic encrusting forms.

3. Although tolerances to environmental conditions ultimately must determine the distributions of *Littorina planaxis* and *L. scutulata,* selection apparently has resulted in behavioral responses which cause avoidance of these limits. *Littorina planaxis* moves up in the field, acting under a strong negative geotaxis. It thus congregates in the highest portions of the splash zone. *Littorina scutulata* shows a similar upshore orientation which keeps it out of low intertidal areas, but this behavioral response is negated by the presence of certain macroscopic algae in the mid-intertidal.

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